

# Infection of red foxes with *Echinococcus multilocularis* in western Switzerland

M. Brossard\*, C. Andreutti and M. Siegenthaler

Institute of Zoology, 11 Rue Emile Argand, CH-2007 Neuchâtel, Switzerland

## Abstract

In the Jura mountains, Plateau and Alps of western Switzerland important variations in the prevalence of *Echinococcus multilocularis* infection in red foxes were observed between geographical areas from 1990 to 1995. The Jura mountains and the Plateau had higher mean prevalence levels than the Alps with 30.6, 32.4 and 18.8%, respectively. The highest rate was recorded in the Plateau in the canton of Fribourg with a prevalence of 52.3%. The prevalence of *E. multilocularis* infection in foxes in the alpine canton of Valais was the lowest (7.1%). Juvenile foxes were found to be more susceptible to *E. multilocularis* than adults. Adult foxes were less heavily infected in summer and autumn, while the prevalence in juveniles (less than 1 year old) increased between the spring and winter, when they are more than 6 months old. The retrospective data relate to the beginning of the 1990s, since when a drastic prevalence increase of *E. multilocularis* infection in foxes has occurred in several regions of Europe. Nevertheless, the study is a major contribution to the epidemiological situation of *E. multilocularis* in central Europe, in that it contains valuable information on spatial distribution and seasonal differences in different age groups of foxes.

## Introduction

Human alveolar echinococcosis has a widespread distribution in the northern hemisphere including Switzerland (Gottstein *et al.*, 1987) and other parts of central Europe (Eckert, 1996). In the vicinity of Switzerland, alveolar echinococcosis has been observed in Austria (Auer & Aspöck, 1991), northern Italy (Casulli *et al.*, 2005), Germany (Daugischies, 1995) and France (Massif Central, Savoie and Franche-Comté) (Petavy *et al.*, 1991). The incidence of human alveolar echinococcosis is low in the European endemic area with 0.02–1.4 new cases per year for 100,000 inhabitants (Eckert, 1996). The causative agent of human alveolar echinococcosis is the larval stage of *Echinococcus multilocularis* (Leuckart) (Cestoda: Cyclophyllidae: Taeniidae). Humans are an aberrant intermediate host, with the disease causing liver pathology. Natural intermediate hosts are wild rodents. The water vole *Arvicola terrestris* and the common vole

*Microtus arvalis* have been found to be infected in Switzerland (Gottstein *et al.*, 1996). The red fox *Vulpes vulpes* is the most important final host, with between 1 and 50% of animals infected (Auer & Aspöck, 1991). Domestic dogs and cats rarely harbour the adult parasite (mostly <1%) in Europe, but dogs are frequently infected in other endemic areas such as China (Budke & Campos-Ponce, 2005). Because the parasite is a severe human pathogen, it is important to evaluate and to characterize the infection of red foxes in Switzerland. In the eastern part of the country, between 5 and 50% of foxes were reported to be infected with *E. multilocularis* (Ewald *et al.*, 1992).

The aim of the present study is to define the prevalence of *E. multilocularis* in red foxes in the cantons of Soleure, Berne, Jura, Neuchâtel, Fribourg, Vaud and Valais (western Switzerland), and to study differences in prevalence between the Jura mountains (mean altitude of 700 m), the Plateau (mean altitude of 600 m) and the Alpine areas of these cantons (mean altitude of 1700 m). Variations of prevalence and intensity of infection with age and gender of the fox, in addition to seasonal patterns of infection, are described.

\*Author for correspondence  
Fax: (41) 32 718 30 01  
E-mail: michel.brossard@unine.ch

## Material and methods

Between October 1990 and May 1995, 3793 red foxes originating from the cantons of Jura, Berne, Soleure, Neuchâtel, Vaud, Fribourg and Valais were examined for *E. multilocularis* infection. Most of them ( $n = 3020$ ) were supplied by the Swiss Centre for Rabies, Bern. The remainder were provided by the Institute Galli-Valerio, Lausanne ( $n = 707$ ) or the Institute of Zoology of the University of Neuchâtel ( $n = 66$ ). The small intestine of each fox was carefully examined for *E. multilocularis* as described by Ewald *et al.* (1992). The small intestine (or the whole fox as necessary) was deep frozen at  $-80^{\circ}\text{C}$  for at least one week to kill the eggs. Diagnosis was achieved by microscopic examination at a  $12\times$  magnification of 15 samples of mucosa which were cut off with microscope slides and prepared in thin layers in Petri dishes. The total length of strobila (1.2–4.5 mm), the form of uterus (sac-like), the position of the genital pore (anterior to middle) and the number of proglottids (2–6) were used as criteria for identification (Thompson, 1986).

The intensity of infection was defined as the number of *E. multilocularis* adults in each infected fox according to Margolis *et al.* (1982). Practically, positive foxes were classified into three classes, namely 1, less than 100 *E. multilocularis* adult worms; 2, from 100 to 1000 worms; and 3, over 1000 worms.

The age, sex and location where foxes were collected were recorded. Fox age, supplied by the Swiss Centre for Rabies, was estimated by X-ray examination of the teeth to measure the relative breadth of the canine cavity (Kappeler, 1985). Foxes were categorized into two age groups, i.e. juveniles, less than one year old, and adults, more than one year old.

### Statistical analysis

Calculation of 95% confidence intervals (CI) of prevalence was performed as described by Newcomb (2004). Pearson's  $\chi^2$  test was used to compare the intensity and the prevalence of *E. multilocularis* infection between geographical areas of western Switzerland, between male and female foxes and to investigate the effect of season on the prevalence of infection in juvenile and adult foxes. Differences were considered significant at  $P < 0.05$ .

## Results

### Prevalence of *E. multilocularis* in red foxes

A total of 3793 red foxes were collected between October 1990 and May 1995 in the Jura mountains (Soleure, Jura, Berne, Neuchâtel and Vaud), the Plateau (Berne, Fribourg and Vaud) and the Alps (Berne, Fribourg, Vaud and Valais) of western Switzerland (table 1 and fig. 1). *Echinococcus multilocularis* adults were found in the intestine of 1142 foxes (30.1%) from all areas. The highest prevalence occurred in the Plateau in the canton of Fribourg (52.3%) and the lowest prevalence was recorded in Valais (7.1%).

Important variations in prevalence values were observed inside and between geographical areas. The prevalence of *E. multilocularis* in foxes varies between different

parts of the Jura mountains. The highest prevalence rates were observed in the north-eastern part (Jura, Berne and Soleure) with 40.5 and 32.7%, respectively and the lowest rates were seen in the south-western part of the region (Neuchâtel and Vaud) with 23.9 and 13.7%, respectively ( $P < 0.01$  to  $P < 0.001$ ). The north-eastern part of the Jura mountains is considered later in the study as a high endemic area and the south-western part of the area as a low endemic area.

Overall, the prevalence of infection in foxes from the Jura mountains (30.6%) did not differ from that of the Plateau (32.4%) ( $P > 0.05$ ) but differed from that of the Alps (18.8%,  $P < 0.001$ ). The prevalence of *E. multilocularis* in the canton of Valais (7.1%) was lower than that observed in other areas of the Alps ( $P < 0.01$  to  $P < 0.001$ ) and in all areas of the Jura mountains and the Plateau ( $P < 0.05$  to  $P < 0.001$ ).

In western Switzerland, infected foxes were observed between the altitude of 300 and 1900 m with the highest prevalence being found between 600 and 1000 m (results not shown).

### Prevalence and intensity of *E. multilocularis* infection, relative to fox age and gender

The age of 3016 foxes was estimated by X-ray examination. The prevalence of *E. multilocularis* was significantly higher in juveniles (34.1%) than in adults (27.6%) (table 2,  $P < 0.001$ ). The intensity of infection was

Table 1. Prevalence of *Echinococcus multilocularis* in red foxes in western Switzerland (1990–1995).

Area	Number of red foxes	Number of positive foxes	Prevalence (CI) %
Jura mountains			
JU + BE	1198	485	40.5 (37.7–43.3) a
SO	211	69	32.7 (26.7–39.3) a
NE	863	206	23.9 (21.1–26.8) a
VD	379	52	13.7 (10.6–17.6) a
Total	2651	812	30.6 (28.9–32.4)
Plateau			
BE	108	24	22.2 (15.4–30.9) b
VD	597	195	32.7 (29.0–36.5) b
FR	86	45	52.3 (41.9–62.6) b,c
Total	791	264	32.4 (30.2–36.7)
Alps			
BE	31	7	22.6 (11.4–39.8)
VD	211	50	23.7 (18.5–29.9)
FR	10	2	20.0 (5.7–51.0)
VS	99	7	7.1 (3.4–13.9) d
Total	351	66	18.8 (15.0–23.2) e
Overall total	3793	1142	30.1 (28.7–31.6)

a,  $P < 0.05$ – $P < 0.001$  between all areas of the Jura mountains; b,  $P < 0.05$ – $P < 0.001$  between all areas of the Plateau; c,  $P < 0.05$ – $P < 0.001$  between the Plateau of Fribourg and all areas of the Jura mountains, the Plateau and the Alps; d,  $P < 0.01$ – $P < 0.001$  between the canton of Valais, the areas of the Jura mountains, the Plateau and the Alps of Berne and Vaud; e,  $P < 0.001$  between the Alps and the Plateau or the Jura mountains.

CI, confidence interval; JU, Jura; BE, Berne; SO, Soleure; NE, Neuchâtel; VD, Vaud; FR, Fribourg; VS, Valais.

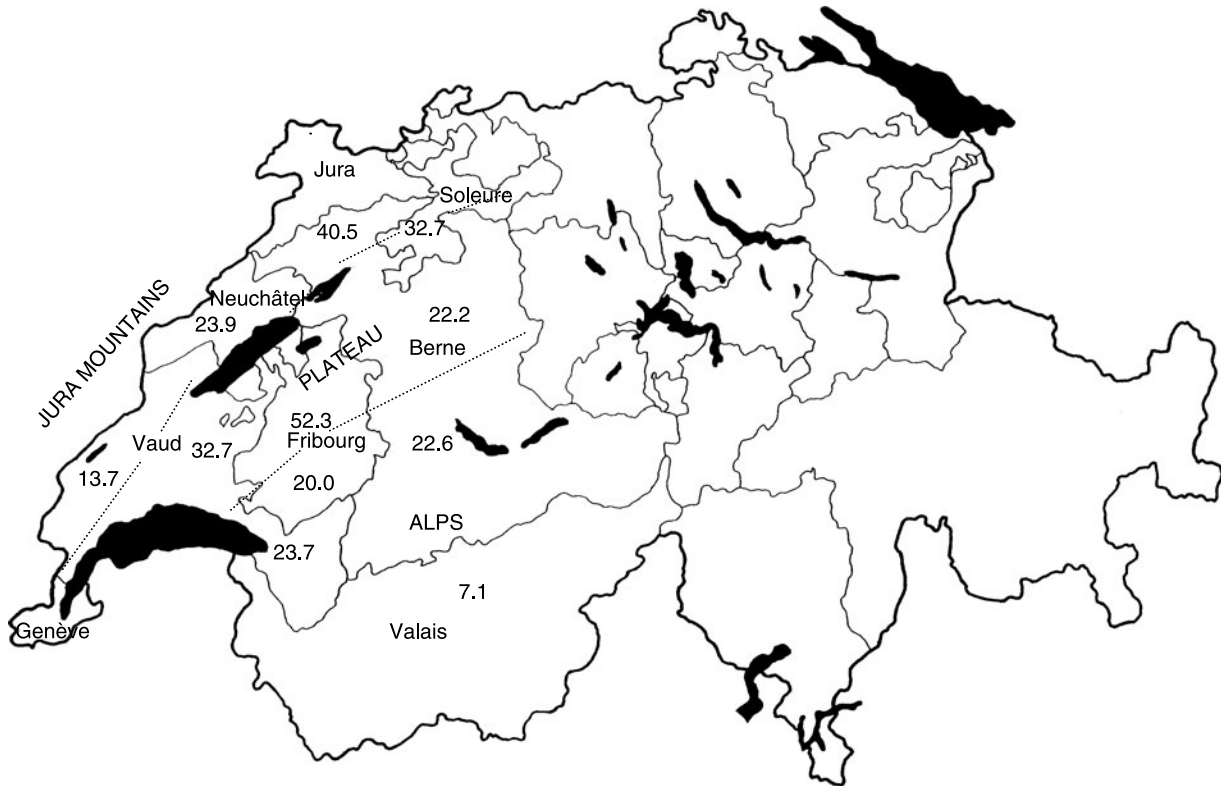


Fig. 1. Prevalence values of *Echinococcus multilocularis* in red foxes in the Jura mountains, the Plateau and the Alps in western Switzerland (1990–1995).

also higher in juveniles where 22.9% of positive individuals were highly infected (class 3) compared to only 8.9% found in adult ( $P < 0.001$ , table 2). Furthermore, 71.1% of adult foxes harboured a lower number of parasites (class 1) than juveniles (51.4%,  $P < 0.001$ ). In the high endemic area of the Jura mountains the infection intensity was also higher in juveniles (6–12 months old) than in adult foxes during October 1991 to March 1992 and October 1992 to March 1993, (fig. 2A,  $P < 0.001$  and  $P < 0.01$ ). In the low endemic area the infection intensity of juvenile foxes was only statistically higher from October 1991 to March 1992 (fig. 2B,  $P < 0.01$ ).

The gender of 3008 foxes was determined, making a total of 1293 females and 1715 males (table 3). No statistical differences were observed between prevalences in female and male foxes (30.2 and 30.9% respectively).

Similarly, there was no difference in the intensity of infection of foxes with *E. multilocularis*, relative to gender.

#### Seasonal variations in *E. multilocularis* infections in juvenile and adult foxes

Data on the prevalence of *E. multilocularis* in juvenile and adult foxes originating from the Jura mountains ( $n = 2212$ ) were collected during three consecutive years, from October 1990 to December 1993. In a first step, results have been grouped and analysed together on a seasonal basis, with juvenile and adult foxes analysed separately (tables 4 and 5).

Nine hundred and eighty juvenile foxes were examined during their first year of life (table 4). In Switzerland, foxes are born at the beginning of spring. In April and May, 2 of

Table 2. Prevalence (%) and intensity of infection of *Echinococcus multilocularis* in juvenile or adult red foxes in western Switzerland (1990–1995).

Age	Degree of infection			Number of infected foxes	Number of analysed foxes
	1	2	3		
Juveniles	244 (51.4%) a	122 (25.7%) b	109 (22.9%) a	475 (34.1%) a CI: 31.6–36.7%	1392
Adults	318 (71.1%)	89 (19.9%)	40 (8.9%)	447 (27.6%) CI: 25.4–29.8%	1621
Total	562 (61%)	211 (22.9%)	149 (16.2%)	922	3016

Degree 1 = <100 worms; 2 = 100–1000 worms; 3 = > 1000 worms; a,  $P < 0.001$ ; b,  $P < 0.05$  between juveniles and adults.

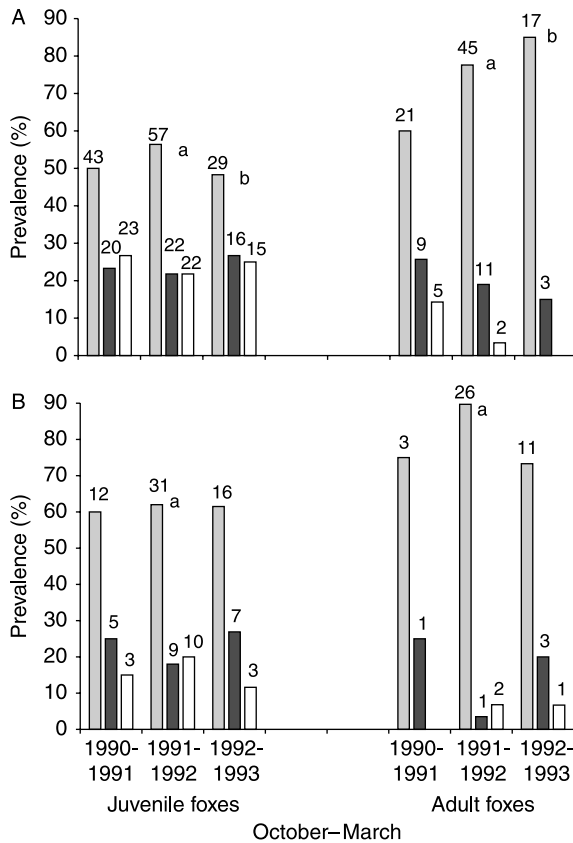


Fig. 2. Intensity of infection of *Echinococcus multilocularis* in foxes from high (A) and low (B) endemic areas of the Jura mountains, Switzerland, in juvenile and adult foxes during 1990 to 1993. a,  $P < 0.001$ ; b,  $P < 0.01$ : significant differences between juvenile and adult foxes between October–March. Number of foxes in each class is indicated. □ degree 1, <100 worms; ■ degree 2, 100–1000 worms; □ degree 3, >1000 worms.

23 young animals were infected but by the beginning of the summer, when foxes were three to four months old, the prevalence had increased to 15.0% ( $P > 0.05$ ), then to 24.0% by August–September ( $P < 0.05$ ). In the autumn (October–November), a sudden and significant increase to 42.0% ( $P < 0.001$ ) was observed followed by a stabilization of prevalence (44.7%) in winter (December–January) ( $P > 0.05$ ), then a decrease in February and March to reach 8.7% in April–May ( $P < 0.01$ ).

In total, 1232 adult foxes were examined (table 5). Statistical differences in prevalences were observed between two periods, i.e. a decrease from 30.7% in April–May to 14.8% in August–September ( $P < 0.01$ ) then a progressive increase from 14.8% to 31.8% in February–March ( $P < 0.001$ ).

In a second step, results of 1990 to 1993 have been analysed on a seasonal and annual basis for the high and low endemic areas in the Jura mountains, with juvenile and adult foxes analysed separately.

The prevalence of *E. multilocularis* infection in young foxes generally increased from spring to winter (April–March) (fig. 3). This tendency was more pronounced in the area of low endemicity. The prevalence of infection in adult foxes of the two areas diminished from spring (April–June) to summer (July–September) and increased again in autumn and winter (from October to March) (fig. 4).

The prevalence of infection in juvenile foxes from the south-western area of the Jura mountains was generally lower than the prevalence in the north-eastern area during 1990 to 1993. The differences are statistically significant for five periods (fig. 3). The prevalence in adult foxes from the south-western area was also often lower than the prevalence from the north-eastern area. The differences are statistically significant for four periods (fig. 4). Although not significant, the prevalence in juvenile foxes increased in the low endemic area in spring 1993 (April–June) and in autumn 1993 (October–December). The same tendency was observed in autumn 1992 and winter 1993 for adult foxes (figs 3 and 4). The last results could indicate an epidemiological modification in a zone that was slightly infected.

## Discussion

*Echinococcus multilocularis* is widespread in the northern hemisphere (North America, north and central Asia and central Europe). In central Europe, infected red foxes (*V. vulpes*) have been reported in Belgium, Luxembourg, France (Massif Central, Savoie and eastern parts), Switzerland, Lichtenstein, Austria, Germany, in northern parts of Poland and in Italy (Eckert, 1996; Deplazes, 2006). Following the success of rabies vaccination (Aubert, 1995), foxes seem to be more abundant and now commonly inhabit urban areas (Stieger *et al.*, 2002). This presents an increased risk of infection to a large human population. The prevalence rates of *E. multilocularis* in fox populations are highly variable regionally and range between <1 and >50%. In the southern (canton of Tessin)

Table 3. Prevalence (%) and intensity of infection of *Echinococcus multilocularis* in female or male red foxes in western Switzerland (1990–1995).

Sex	Degree of infection			Number of infected foxes	Number of analysed foxes
	1	2	3		
Female	228 (58.3%)	98 (25.1%)	65 (16.6%)	391 (30.2%) CI: 27.8–32.8%	1293
Male	333 (62.8%)	113 (21.3%)	84 (15.8%)	530 (30.9%) CI: 28.7–33.2%	1715
Total	561	211	149	921	3008

Degree 1 = <100 worms; 2 = 100–1000 worms; 3 = >1000 worms;  $P > 0.05$ .



Table 4. The prevalence (%) of *Echinococcus multilocularis* in juvenile foxes in western Switzerland during 1990 to 1995.

Months	Number of foxes	Number of positive foxes	Prevalence (CI) %
April–May	23	2	8.7 (1.5–29.5) a
June–July	147	22	15.0 (9.8–22.0) b,c
August–September	104	25	24.0 (16.4–33.6) c,d
October–November	231	97	42.0 (35.6–48.6) a,b,d
December–January	266	119	44.7 (38.7–51.0) a,b
February–March	209	79	37.8 (31.3–44.8) a,b
Total	980	344	35.1 (32.1–38.2)

CI, confidence interval. a,  $P < 0.01$ ; b,  $P < 0.001$ ; c,  $P < 0.05$ ; d,  $P < 0.01$ : significant differences between the monthly periods.

and eastern parts of Switzerland 2 and 50% of foxes are infected, respectively (Deplazes *et al.*, 1992). In the present work we studied the *E. multilocularis* infection of red foxes in the western part of Switzerland between 1990 and 1995 (cantons of Soleure, Berne, Jura, Neuchâtel, Fribourg, Vaud and Valais). Infected foxes were observed in all cantons studied and at altitudes from 300 to 1900 m, with the highest prevalence recorded between 600 and 1000 m. Human alveolar echinococcosis was specially mentioned in northern Switzerland (Gottstein *et al.*, 1987). Nevertheless, foxes were also infected south of the Jura mountains on the Swiss Plateau (32.4%) and in the Alps (18.8%). In the isolated alpine canton of Valais, 7.1% of foxes were still infected. In the canton of Geneva, the prevalence decreased from the rural and residential areas (52 and 49% respectively) to urban areas (prevalence of 31%) (Fischer *et al.*, 2005). In several regions of Europe, a drastic prevalence increase has occurred since the early 1990s (Vuitton *et al.*, 2003). This might account for the differences between the low rates given for western Vaud (13.7%), and the high rates cited for neighbouring Geneva obtained a decade later (Fischer *et al.*, 2005). As shown in the present study, the prevalence of infection in foxes of the south-western area of the Jura mountains increased from 1990 to 1993 and became comparable with that of the high endemic area of the north-eastern part (figs 3 and 4). In southern Germany, a long-term increase in the prevalence of *E. multilocularis* in foxes was reported, with a more widespread distribution than previously thought

(Lucius & Bilger, 1995). Despite high prevalences in foxes, alveolar echinococcosis in humans is relatively rare. In Switzerland, a relatively stable annual morbidity rate of 0.18 cases per 100,000 inhabitants was recorded in recent decades, with high annual incidence rates occurring more regionally, as observed in the Swiss canton of Jura (0.74/100,000) (Gottstein *et al.*, 1987, Ammann *et al.*, 1999, Kern *et al.*, 2003). From 1990 to 1993 we studied the infection of foxes from the Jura mountains, which constitute an area adjacent to the endemic Doubs department in France (Bresson-Hadni *et al.*, 1994). The prevalence of the infection decreases from 40.5% in the canton of Jura and Berne (north-eastern area of the Jura mountains) to 13.7% in the north of the canton of Vaud (south-western area of the Jura mountains). A decrease in prevalence is spatially regular and could be explained by region differences in density of arvicolid species and prevalence of *E. multilocularis* metacystodes in the intermediate host. On the other hand the geology (altitudes), vegetation and the climate are all similar in the Jura range.

The only free living stage of *E. multilocularis* is the egg which survives better under cold than warm temperatures (Veit *et al.*, 1995). These authors performed an interesting experiment in south-western Germany. *Echinococcus multilocularis* eggs were sealed into bags of nylon mesh and exposed there to the natural climate during various seasons. The maximal survival time was 240 days from autumn to spring but only 78 days in summer. Accordingly, the prevalence of *E. multilocularis*

Table 5. The prevalence (%) of *Echinococcus multilocularis* in adult foxes in western Switzerland during 1990 to 1995.

Months	Number of foxes	Number of positive foxes	Prevalence (CI) %
April–May	114	35	30.7 (22.6–40.1) a,b
June–July	314	64	20.4 (16.1–25.3) a
August–September	122	18	14.8 (9.2–22.6) b,c,d,e
October–November	175	44	25.1 (19.4–32.4) c
December–January	262	79	30.2 (24.7–36.2) d
February–March	245	78	31.8 (26.1–38.1) e
Total	1232	318	25.8 (23.4–28.4)

CI, confidence interval. a,  $P < 0.05$ ; b,  $P < 0.01$ ; c,  $P < 0.05$ ; d,  $P < 0.01$ ; e,  $P < 0.001$ : significant differences between the monthly periods.

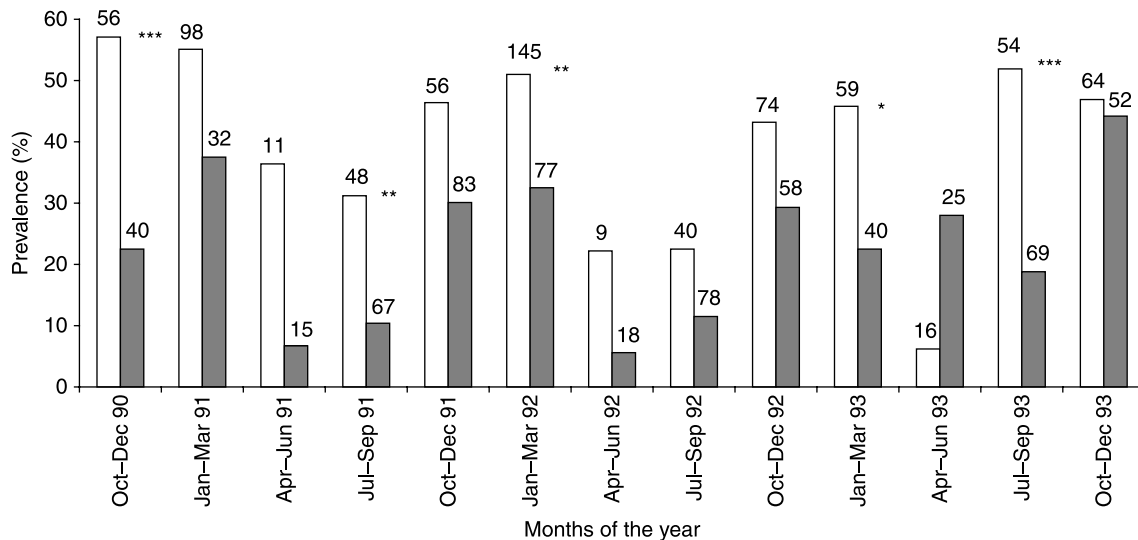


Fig. 3. The prevalence (%) of *Echinococcus multilocularis* in juvenile foxes during 1990 to 1993 in a high (□) or low (■) endemic area in the Jura mountains, Switzerland. Number of foxes in each class is indicated. \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ : significant differences between high and low endemic areas.

in adult foxes of western Switzerland was less pronounced during the second half of summer than in autumn and winter. The seasonal vole population densities, and the seasonal size of the fox population, with the resulting differences in egg production could also influence the seasonal prevalence of infection. Small mammals (Insectivora and Rodentia) are the intermediate hosts of *E. multilocularis*. In central Europe, the common vole *M. arvalis* and the water vole *A. terrestris* are important in transmission. As shown in the Doubs department (France), human alveolar echinococcosis is

strongly influenced by the densities of arvicolid species (Viel *et al.*, 1999). In Switzerland, water and common voles also seem to be important intermediate hosts (Gottstein *et al.*, 1996, 2001). In a small area of the Plateau in canton of Fribourg *E. multilocularis* metacystode was found in 10–39% of an *A. terrestris* population and in 10–23% of an *M. arvalis* population during six seasons of investigation (1993–1998). A high prevalence ranging between 47% and 56% was consistently determined in the fox population of that area during 1993 and 1994, respectively.

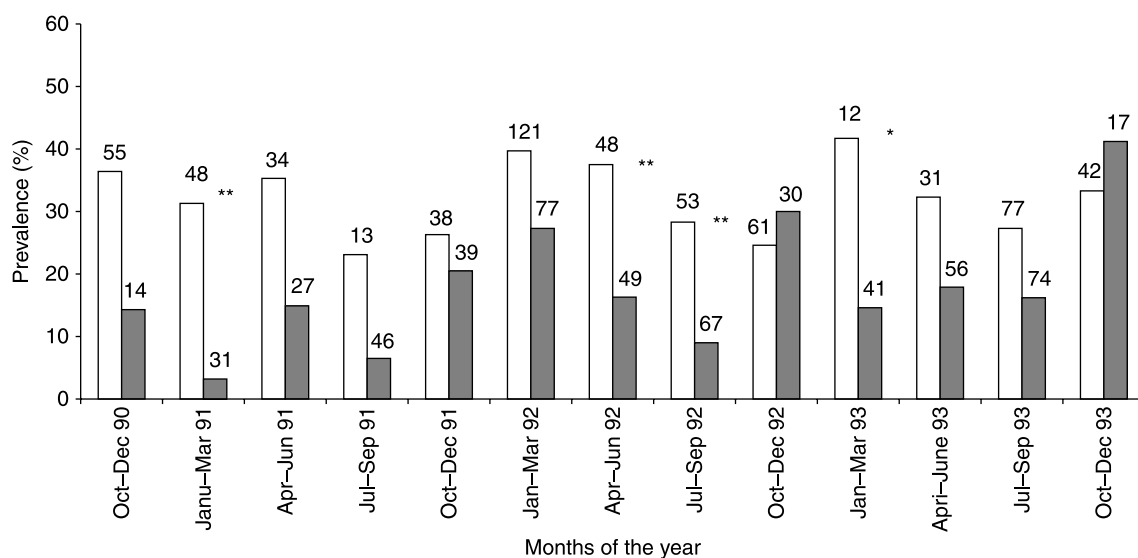


Fig. 4. The prevalence (%) of *Echinococcus multilocularis* in adult foxes during 1990 to 1993 in a high (□) or low (■) endemic area in the Jura mountains, Switzerland. Number of foxes in each class is indicated. \* $P < 0.05$ , \*\* $P < 0.01$ : significant differences between high and low endemic areas.

Young foxes (less than 1 year old) were more frequently and more intensely infected by *E. multilocularis* than in older animals. In the high endemic area of the Jura mountains, prevalence and intensity of infection were lower in adult than in juvenile foxes. This may be due to parasite-induced host immunity to reinfection. This phenomenon was also observed in other studies (Hofer *et al.*, 2004) and was also seen in dogs infected with *E. granulosus* (Torgerson *et al.*, 2004).

In brief, the prevalence of *E. multilocularis* in foxes of the Jura mountains and the Plateau was higher than that recorded in foxes in the Alps, with important variations inside each geographical area. Between 1990 and 1995, the highest rate was recorded in the Plateau in the canton of Fribourg with a prevalence of 52.3%. Moreover, the prevalence of *E. multilocularis* infection in foxes in the alpine canton of Valais was the lowest (7.1%). Young foxes were more often and more intensively infected than the adults.

### Acknowledgements

The authors thank the Swiss Centre for Rabies, the Galli-Valerio Institute in Lausanne for providing intestines of red foxes, the Swiss Federal Office for Public Health and Wildlife Protection Service of Cantor Vaud for their financial support, and Dr P. Torgesson for critically reviewing the manuscript.

### References

- Ammann, R.W., Fleiner Hoffmann, A. & Eckert, J. (1999) Schweizerische Echinokokkose-Studiengruppe (SESG). Schweizerische Studie (SESG). Schweizerische Studie für Chemotherapie der alveolären Echinokokkose-Rückblick auf ein 20 jähriges klinisches Forschungsprojekt. *Schweizerische Medizinische Wochenschrift* **129**, 323–332.
- Aubert, M. (1995) Epidemiology and campaign against rabies in France and Europe. *Bulletin de l'Académie Nationale de Médecine* **179**, 1033–1054.
- Auer, H. & Aspöck, H. (1991) Incidence, prevalence and geographic distribution of human alveolar echinococcosis in Austria from 1854 to 1990. *Parasitology Research* **77**, 430–436.
- Bresson-Hadni, S., Laplante, J.J., Lenys, D., Rohmer, P., Gottstein, B., Jacquier, P., Mercet, P., Meyer, J.P., Miguet, J.P. & Vuitton, D.A. (1994) Seroepidemiologic screening of *Echinococcus multilocularis* infection in a European area endemic for alveolar echinococcosis. *American Journal of Tropical Medicine and Hygiene* **51**, 837–846.
- Budke, C.M. & Campos-Ponce, M. (2005) A canine purgation study and risk factor analysis for echinococcosis in a high endemic region of the Tibetan plateau. *Veterinary Parasitology* **127**, 43–49.
- Casulli, A., Manfredi, M.T., La Rosa, G., Di Cerbo, A.R., Dinkel, A., Romig, T., Deplazes, P., Genchi, C. & Pozio, E. (2005) *Echinococcus multilocularis* in red foxes (*Vulpes vulpes*) of the Italian Alpine region: is there a focus of autochthonous transmission? *International Journal for Parasitology* **35**, 1079–1083.
- Dauguschies, A. (1995) Importance of epidemiology and control of the fox tapeworm, *Echinococcus multilocularis*, in Germany. *Deutsche Tierärztliche Wochenschrift* **102**, 306–310.
- Deplazes, P. (2006) Ecology and epidemiology of *Echinococcus multilocularis* in Europe. *Parassitologia* **48**, 37–39.
- Deplazes, P., Gottstein, B., Eckert, J., Jenkins, D.J., Ewald, S.J. & Jimenez-Palacios, S. (1992) Detection of *Echinococcus* coproantigens by enzyme-linked immunosorbent assay in dogs, dingoes and foxes. *Parasitology Research* **78**, 303–308.
- Eckert, J. (1996) The 'dangerous fox tapeworm' (*Echinococcus multilocularis*) and alveolar echinococcosis of humans in central Europe. *Berliner und Münchener Tierärztliche Wochenschrift* **109**, 202–210.
- Ewald, D., Eckert, J., Gottstein, B., Straub, M. & Nigg, H. (1992) Parasitological and serological studies on the prevalence of *Echinococcus multilocularis* Leuckart, 1863 in red foxes (*Vulpes vulpes* Linnaeus, 1758) in Switzerland. *Scientific and Technical Review* **11**, 1057–1061.
- Fischer, C., Reperant, L.A., Weber, J.M., Hegglin, D. & Deplazes, P. (2005) *Echinococcus multilocularis* infections of rural, residential and urban foxes (*Vulpes vulpes*) in the canton of Geneva, Switzerland. *Parasite* **12**, 339–346.
- Gottstein, B., Lengeler, C., Bachmann, P., Hagemann, P., Brossard, M., Witassek, F. & Eckert, J. (1987) Seroepidemiological survey for alveolar echinococcosis (by Em2-ELISA) of blood donors in an endemic area of Switzerland. *Transactions of the Royal Society of Tropical Medicine and Hygiene* **81**, 960–964.
- Gottstein, B., Saucy, F., Wyss, C., Siegenthaler, M., Jaquier, P., Schmitt, M., Brossard, M. & Demierre, G. (1996) Investigations on a Swiss area highly endemic for *Echinococcus multilocularis*. *Applied Parasitology* **37**, 129–136.
- Gottstein, B., Saucy, F., Deplazes, P., Reichen, J., Demierre, G., Busato, A., Zuercher, C. & Bugin, P. (2001) Is high prevalence of *Echinococcus Multilocularis* in wild and domestic animals associated with disease incidence in humans? *Emerging Infectious Diseases* **7**, 408–412.
- Hofer, S., Gloor, S., Müller, U., Mathis, A., Hegglin, D. & Deplazes, P. (2004) High prevalence of *Echinococcus multilocularis* in urban red foxes (*Vulpes vulpes*) and voles (*Arvicola terrestris*) in the city of Zürich, Switzerland. *Parasitology* **120**, 135–142.
- Kappeler, A. (1985) Untersuchungen zur Alterbestimmung und zur Altersstruktur verschiedener Stichproben aus Rotfuchs-Populationen (*Vulpes vulpes* L.) in der Schweiz. PhD thesis, Institute of Zoology, University of Berne.
- Kern, P., Bardonnet, K., Renner, E., Auer, H., Pawlowski, Z., Ammann, R.W., Vuitton, D.A. & Kern, P. (2003) European echinococcosis registry: human alveolar echinococcosis, Europe, 1982–2000. *Emerging Infectious Diseases* **9**, 343–349.
- Lucius, R. & Bilger, B. (1995) *Echinococcus multilocularis* in Germany: increased awareness or spreading of a parasite. *Parasitology Today* **11**, 430–434.
- Margolis, L., Esch, G.W., Holmes, J.C., Kuris, A.M. & Schad, G.A. (1982) The use of ecological terms in parasitology

- (report of an ad hoc committee of the American Society of Parasitologists). *Journal of Parasitology* **68**, 131–133.
- Newcomb, R.G.** (2004) Two-sided confidence intervals for the single proportion: comparison of seven methods. *Statistics in Medicine* **17**, 857–872.
- Petary, A.F., Deblock, S. & Walbaum, S.** (1991) Life cycles of *Echinococcus multilocularis* in relation to human infection. *Journal for Parasitology* **77**, 133–137.
- Stieger, C., Hegglin, D.F., Schwarzenbach, G.F., Mathis, A.F. & Deplazes, P.** (2002) Spatial and temporal aspects of urban transmission of *Echinococcus multilocularis*. *Parasitology* **124**, 631–640.
- Thompson, R.C.A.** (1986) *The biology of echinococcus and hydatid disease*. London, Boston & Sydney, George Allen & Unwin.
- Torgerson, P.R., Shaikenov, B.S., Rysmukhambetova, A.T., Ussenbayev, A.E., Abdybekova, A.M. & Burtisurnov, K.K.** (2004) Modelling the transmission dynamics of *Echinococcus granulosus* in dogs in rural Kazakhstan. *Parasitology* **126**, 417–424.
- Veit, P., Bilger, B., Schad, V., Schafer, J., Frank, W. & Lucius, R.** (1995) Influence of environmental factors on the infectivity of *Echinococcus multilocularis* eggs. *Parasitology* **110**, 79–86.
- Viel, J.F., Giraudoux, P., Abrial, V. & Bresson-Hadni, S.** (1999) Water vole (*Arvicola terrestris* Scherman) density as risk factor for human alveolar echinococcosis. *American Journal of Tropical and Medical Hygiene* **61**, 559–565.
- Vuitton, D.A., Zhou, H., Bresson-Hadni, S., Wang, Q., Piarroux, M., Raoul, F. & Giraudoux, P.** (2003) Epidemiology of alveolar echinococcosis with particular reference to China and Europe. *Parasitology* **127** (Suppl.), S87–107.

(Accepted 8 February 2007)

© 2007 Cambridge University Press